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Effects of Timber Harvest on Soil Properties and Forest Recovery of Subalpine Beetle Kill Forests of Northwestern Colorado

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EFFECTS OF TIMBER HARVEST ON SOIL PROPERTIES AND FOREST RECOVERY OF
SUBALPINE BEETLE KILL FORESTS OF NORTHWESTERN COLORADO

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Abstract

Mortality caused by mountain pine beetle and spruce beetle have together affected vast areas of forest in Northwestern Colorado throughout the last 15 years. In the midst of such a widespread bark beetle epidemic, it is crucial that land management agencies such as the USDA Forest Service understand how different forest types are responding to these natural disturbance events that have historically played an ecologically important role, in order to foster the future resilience of these forests. Particularly, it is practical and important to develop an understanding of how the bark beetle disturbances are interacting with management strategies such as timber harvest. The purpose of the present study was to investigate the influences of multiple disturbances on soil physical and chemical properties, as well as the successional trajectory of a mixed subalpine forest. Thirty plots were established with 10 in each of three treatments, consisting of forests of bark beetle induced mortality (beetle kill), logged beetle kill forests, and intact/green (control) forests. In each plot, soil samples were collected and number/species of seedlings, fractional cover of forest understory, coarse woody debris, and canopy trees were measured and recorded. While forest conditions do not differ substantially between forests subject to beetle kill and intact/green forests, in many instances, harvesting of beetle kill stands is altering soil properties and forest understory conditions such that the dominance of subalpine fir establishment/accelerated growth associated with forests of high beetle mortality is suppressed, and no alternative successional trajectory is favored as of now.

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INTRODUCTION:

Extent of Beetle Mortality and Implications

Current bark beetle infestations in Colorado are extensive. Mortality caused by mountain pine beetle (*Dendroctonus ponderosae*) has affected 247,263 hectares in Northwestern Colorado from 1996-2011 (Harris et al. 2012), and mortality from spruce beetle (*Dendroctonus rufipennis*) has affected 64,345 hectares in Northwestern Colorado from 1996-2011 (Harris et al. 2012) (Fig. 1). Both beetles are native insects and typically infest lodgepole pine (*D. ponderosae*) and large diameter Engelmann spruce trees (*D. rufipennis*), respectively. However, the current infestation is of such great proportions that considerable attention has focused on its broader impacts on forests and the services forests provide.

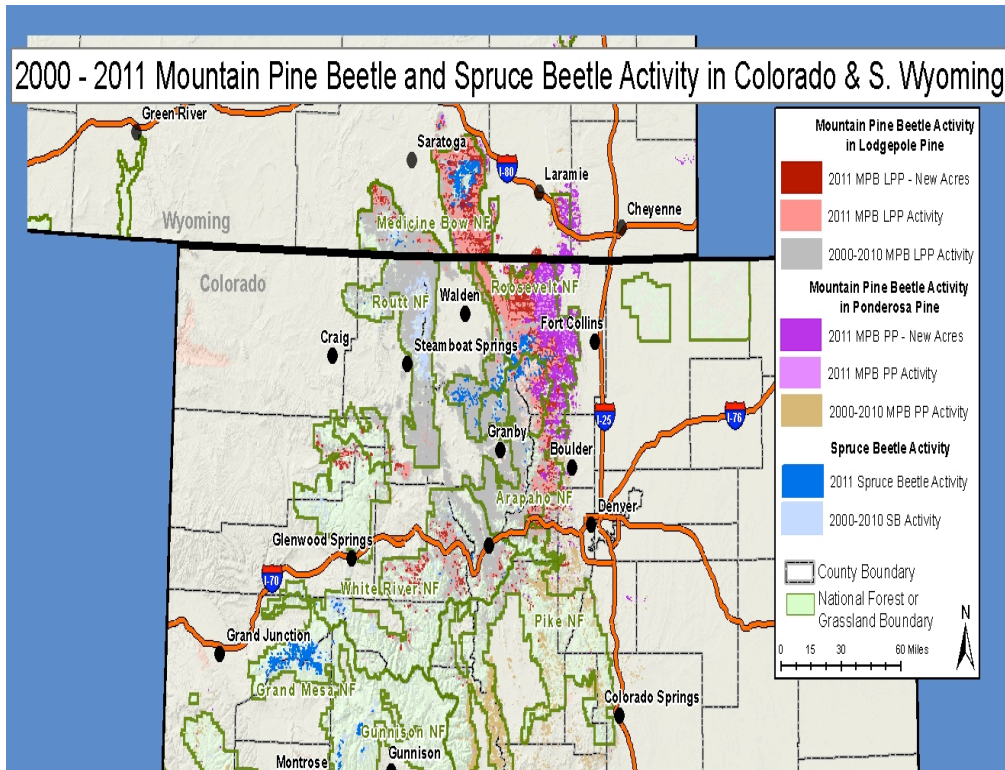


Figure 1: Mountain pine beetle and spruce beetle activity in Northern Colorado and Southern Wyoming from 2000-2011 (Harris et al. 2012). This map is a product of aerial surveys only displaying areas and year of mortality. It does not include infested areas that are not detectable via aerial surveys, nor does it indicate level of mortality.

Understanding how subalpine forests impacted by these widespread insect infestations are likely to respond to the disturbance is crucial to understanding which, if any, land management strategies must be taken. One current strategy in forests of high bark beetle induced mortality (beetle kill forests) is harvesting of dead timber (for the purposes of either salvage, hazard tree removal, or proactive management to influence future forest conditions). The impact of timber harvest in beetle kill stands must be well understood if land management agencies are to foster the resilience of these forests.

Disturbance Interactions in Subalpine Forests and Study Significance

Subalpine ecosystems in the Rocky Mountains are shaped by natural disturbances in space (pattern) and time (succession) (Veblen 1998). Characteristics such as frequency and severity define the disturbances that drive spatial and temporal patterns in a landscape (Paine and Levin 1981; Turner et al. 1993). In subalpine ecosystems, where much of the current stand structure is a result of past natural disturbance events (such as fire, insect outbreaks, and windthrow), it is interesting to consider what the effects of unique or novel interactions between natural disturbances and anthropogenic disturbances might be. In the Routt National Forest of Northern Colorado, insect outbreaks, windthrow, past fires, and logging are disturbances that interact to form unique patterns and processes in a subalpine ecosystem (Veblen 1998; Kulakowski and Veblen 2002; Bebi et al. 2003; Rumbaitis-del Rio 2006; Buma and Wessman 2011).

An understanding of the interactions among multiple disturbance events will be crucial in determining the future characteristics of these forests, and ultimately developing plans to enhance their resilience to future disturbances. Resilient forests are important for an array of reasons, notably for the ecosystem services they provide. For example, forests are an important carbon sink. Additionally, humans rely on healthy forests for economic benefit, whether through natural resource utilization, or through a forest-based tourism industry. So, it is important that forests are capable of persisting through novel disturbance events created by interactions between disturbances (Buma and Wessman 2011), and in particular

natural and human disturbances. In order to foster this resilience, we must first understand how multiple disturbances are affecting the forest ecosystem. With this knowledge, predictions can be made about future forest structure, which is crucial to making informed management decisions after disturbances occur (Kayes and Tinker, 2012).

Study Objectives, Questions, and Hypotheses

The objective of the present study was to investigate the interaction between beetle infestations and timber harvest by quantifying their individual and combined effects on soil physical and chemical properties, as well as on the successional trajectory of the forest following disturbance. Many studies have been published in recent years investigating predominantly lodgepole pine forest response to the widespread mountain pine beetle epidemic, and several studies have investigated forest stand dynamics and response to spruce beetle infestation (Collins et al. 2011; Diskin et al. 2011; Veblen et al. 1991). The present study investigates the influence of both mountain pine beetle and spruce beetle in a forest canopy containing some lodgepole pine (*Pinus contorta*), but dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Additionally, there have been a small number of recent investigations into the impacts of logging operations on beetle kill forests in the current epidemic (Collins et al. 2011; Griffin et al. 2013). The present study seeks to expand on this area of research. It is important to understand how ecosystem properties are responding to beetle infestations, and particularly how this natural disturbance and management strategies (such as

timber harvest) are interacting, considering the severity and broad extent of current epidemics.

With all of these interactions in mind, the following questions were investigated:

Q₁: Are soil physical properties of forests subject to beetle kill different from intact/green forests, and are they altered when logging occurs?

H₁: Soil physical properties such as bulk density, soil moisture, organic horizon mass, and soil horizon depths will all be different among the three treatments (beetle kill, logged beetle kill, and control group) due to the increase of forest floor organic matter and reduced evapotranspiration associated with beetle kill forests, as well as the disruption associated with logging equipment and the complete exposure of the forest understory after the logging event.

H₀: There are no differences in soil physical properties among treatments.

Q₂: Are soil chemical properties of forests subject to beetle kill different from intact/green forests, and are they altered when logging occurs?

H₂: Soil chemical properties such as carbon (Mg/Ha), nitrogen (Mg/Ha), and C:N ratios will differ among the three treatments due to plant material added to the

forest floor from beetle kill trees, and the soil disruption/mixing associated with logging.

H₀: Soil chemical properties will not differ among the three treatments.

Q₃: Is beetle kill of such great magnitude changing forest succession, and composition of forest understory? Does logging alter this trajectory?

H_{3.1}: Logging beetle kill forests results in a unique disturbance interaction that changes conditions of the ecosystem such that total and per species seedling densities are lower after harvest, and species composition is different between beetle kill stands and harvested beetle kill stands (resulting in a shift in successional trajectory associated with logging).

H_{3.2}: Logging beetle kill forests creates new environmental conditions that result in differential forest understory growth from that of beetle kill and intact/green forests due to disruption of soil, the loss of forest canopy, and increased light levels.

H₀: There will be no differences among treatments in seedling densities or forest understory composition.

Study Predictions

Specifically, I predicted that bulk density (a measure of soil compaction) would be highest in the logged beetle kill forests (and that the treatment subject to beetle kill and control forests would have similar bulk densities); that soil moisture would be highest in the beetle kill treatment and lowest in the logged beetle kill treatment; and that organic horizon mass, duff, and organic horizons in the beetle kill treatment would exceed that of the logged beetle kill treatment and control forests, and would be lowest in the logged beetle kill treatment. I also expected to find that soil carbon and nitrogen would be lower in the logged beetle kill treatment than the beetle kill treatment or control forests, and highest in the beetle kill forests. I expected to find differences in overall seedling densities among the treatments, and, in particular, that subalpine fir seedling densities in the beetle kill treatment would far exceed those of the logged beetle kill treatment or control forests (because subalpine fir is a shade tolerant early successional species), whereas lodgepole pine seedling densities in the logged beetle kill treatment would exceed that of the beetle kill treatment or control forests (due to drier, more exposed conditions). I also predicted that the percent of coarse woody debris, bare soil, and graminoids on the forest floor would be highest in the logged beetle kill treatment, while percent of forbs on the forest floor would dominate in the beetle kill treatment, compared to the logged beetle kill treatment or control forests.

BACKGROUND:

Bark Beetle Ecology and Forest Response

Lodgepole pine mortality from mountain pine beetle, as well as Engelmann spruce mortality from spruce beetle, are natural disturbances currently very prevalent on the Routt National Forest of Northwestern Colorado. Bark beetles tend to attack larger trees that are at least 10 to 20 cm in diameter, and attacks are usually lethal (Veblen 1998). Periodically, populations of mountain pine beetle can reach epidemic proportions (Roe and Amman 1970) and kill the overstory trees in entirety over a large region (Schmid and Mata 1996).

Historically, the mountain pine beetle has played an important role in the ecology of lodgepole pine forests (Logan and Powell 2001), since infestations of mountain pine beetle might be an important mechanism of change in the structure of these forests or might play a role (but don't serve as a mechanism) in the intense crown-replacing fires that drive lodgepole pine reproduction (Logan and Powell 2001). While mortality from mountain pine beetle does not result in an immediate loss of the overstory canopy (Collins et al. 2011), light levels on the forest floor increase with loss of needles and even more so with the eventual fall of the canopy trees. The lack of exposure of mineral soil, coupled with the remaining bits of forest canopy associated with beetle kill forests, may favor the establishment or release (accelerated understory growth) of species that are shade tolerant (such as subalpine fir, Engelmann spruce, and aspen) over lodgepole pine (Veblen 1998; Claveau et al. 2002), which in turn may mean greater forest heterogeneity.

Specifically, death of lodgepole pine in the forest overstory may speed succession toward Engelmann spruce and subalpine fir, which are more shade tolerant species (Veblen 1998).

The spruce beetle has also played a historically important role in the ecology of subalpine forests (Baker and Veblen 1990; Veblen 1998). Spruce beetle outbreaks tend to occur after large blowdown events (Schmid and Frye 1977) and may target large diameter spruce trees (Alexander 1987; Schmid and Mata 1996), resulting in a shift of forest stand structure from spruce to fir as the predominant conifer (Veblen et al. 1991). The beetle outbreak allows for previously existing seedlings in the understory to grow (Veblen et al. 1991).

It appears as though subalpine forests are resilient to beetle infestations, as multiple studies have shown substantial forest regeneration following disturbance (Diskin et al. 2011; Collins et al. 2011; Kayes and Tinker 2012). While successional trajectories of beetle-infested forests are likely to depend on various stand characteristics prior to the disturbance event (i.e. species dominant in the forest canopy) (Diskin et al. 2011), lodgepole pine may remain the predominant species (in those forests where it was present prior to disturbance) in places where seed sources for more shade tolerant species are limited, or where other environmental conditions are less favorable to the success of other species (Amman 1977; Sibold et al. 2006). In stands dominated by Engelmann spruce prior to the spruce beetle infestation, there also may ultimately be a return to this dominance, due to the

oscillations in stand structure (that may be a result of subalpine fir response time and Engelmann spruce life span) associated with subalpine forests (Veblen et al. 1991).

While it is still unclear exactly what the developmental trajectory of mixed Engelmann spruce, subalpine fir, and lodgepole pine subalpine forests is in response to the current beetle outbreaks (Diskin et al. 2011), this mixed forest type shows the highest post-disturbance basal area and seedling density of all overstory types impacted by bark beetles (Diskin et al. 2011). Clearly, in a subalpine forest, the current mountain pine beetle and spruce beetle outbreaks are by no means a barrier to new growth.

Multiple Disturbance Events: Consequences of Beetle Kill and Harvest for Successional Trajectories

While insect outbreaks are a natural component of the disturbance regime characterizing subalpine forests (Veblen 1998), logging of disturbed sites may disrupt forest conditions (e.g. soil, seedlings), thereby shifting successional trajectory away from what it would have been naturally (Lindenmayer and Noss 2006). In disturbed forests, such as those impacted by mountain pine beetle and spruce beetle, there may be human interest in salvaging the dead timber for numerous purposes. In areas allocated for timber production, there may be an economic interest in making use of timber resources. Near areas of human use or communities, there may be an interest in mitigating fire hazards or easing future

fire suppression efforts by changing fuel loads. Over broad areas, there may be a desire to influence future forest stand composition to meet a variety of objectives. Logging might also be simply for the purpose of removing hazardous dead trees.

However, when a disturbed forest undergoes the additional disturbance of salvage harvesting, the interaction of the two disturbances has potential for serious negative impacts on the ecosystem as a whole, and its living components (Lindenmayer et al. 2008). Ecosystem processes may be altered by the combined effects of natural and anthropogenic disturbances, resulting in an altered ecosystem response (Lindenmayer and Noss 2006).

It is clear that logging has a consequence for the future of a beetle kill forest. Collins et al. (2011) showed that in logged stands of beetle-infested lodgepole pine dominated subalpine forests, lodgepole pine will likely remain the dominant species over the next century, while in forests that are not harvested, subalpine fir will likely become the most abundant species. Because beetle infestation may favor accelerated growth of previously existing shade tolerant seedlings (Collins et al. 2011; DeRose and Long 2010; Veblen 1986), and given the fact that logging tends to eliminate most advanced regeneration, new seedling establishment is likely to be the most important source of new growth in logged beetle kill stands (Collins et al. 2011). Drier, more exposed conditions, characterized by increased exposure of bare mineral soil from harvesting activities, favor establishment of lodgepole pine seedlings (Lotan 1964; Lotan 1975; Lotan and Perry 1983). Harvesting of beetle-

infested forests may thus change the conditions of the forest such that shifts in successional trajectory occur. While the forest canopy structure in the study by Collins et al. (2011) is slightly different (as lodgepole pine is a co-dominant canopy species as opposed to a sub-dominant canopy species), both studies were done in a subalpine ecosystem, so it is interesting to consider how the impacts of logging subalpine beetle kill forests compare.

Multiple Disturbance Events: Impacts of Beetle Kill and Harvest on Soil Properties

Soil chemical and physical properties play an important role in the structure and functioning of the ecosystem, and ultimately forest composition and growth.

Harvesting may disrupt these properties. Edaphic factors influence the longevity of seeds (Pakeman et al. 2011). The organic horizon is the layer in which seedlings establish, and various soil chemical and physical properties both influence, and are influenced by, the type and abundance of vegetation in forest ecosystems.

Essentially, soils play a very important role in the development of forests, as they are the source of support, moisture, and nutrients for trees in a forest ecosystem.

Soil structure, horizon depths, and organic matter provide insight into viability of soils for vegetation establishment.

However, there may be important changes to soil properties with logging. Because salvage logging often occurs in an area with fallen trees, timber removal tends to be a difficult task, which usually leads to more soil disruption (Holtam, 1971). Similar to a beetle kill forest, forests that have experienced blowdown from wind are

characterized by increased light levels and environmental heterogeneity, which allow for the establishment of greater species diversity in the understory (Peterson and Pickett, 1995). A study by Rumbaitis-del Rio (2006) on a large blowdown in northern Colorado found that areas of blowdown that were subsequently logged had, in comparison to unlogged blowdown, lower understory species cover and diversity, a shallower organic soil horizon, and greater coverage of bare mineral soil (all of which led to differences in nitrogen (N) content in organic horizon and mineral fractions in blowdown/salvage-logged plots versus control or blowdown plots; Rumbaitis-del Rio 2006). While blowdown and beetle kill are very different disturbances, the fact that they result in similar conditions of increased light levels and environmental heterogeneity suggests the potential for similar disruption of soil properties following timber harvest in beetle kill stands.

Logging of a disturbed ecosystem is likely to cause changes in the development of the soil profile, as well as changes in nutrient cycling (Lindenmayer and Noss, 2006). Clow et al. (2011) found that soils under beetle kill trees (in a predominantly lodgepole pine forest) are moister than soils under undisturbed trees, perhaps due to reduced evapotranspiration resulting from tree death. However, this distinction might not hold true for beetle kill forests that were subsequently logged. Soil carbon:nitrogen ratios have not been found to differ significantly between beetle kill and control forest stands (Griffin et al. 2011), however it is interesting to consider how soil chemical properties might differ between disturbed and undisturbed when the additional disturbance of logging is added (perhaps creating unique

interactions). Clow et al. (2011) found that while nitrogen content was higher under beetle kill trees than undisturbed trees, these differences were relatively minor considering the widespread extent of beetle mortality in their study area. Once again, this raises the question of whether multiple disturbances are likely to enhance the difference between disturbed and undisturbed stands. Griffin et al. (2013) specifically found that in beetle kill stands, soil nitrate concentrations differed in harvested areas of beetle-infected trees, indicating that multiple disturbances may be altering important soil chemical properties.

METHODS:

Study Area

The study area was subalpine forest of the Routt National Forest, located in northwestern Colorado north of Steamboat Springs, on the Hahns Peak Bears Ears Ranger District (Fig. 2). The main canopy species of these subalpine forests are Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*), with some trembling aspen (*Populus tremuloides*), and lodgepole pine (*Pinus contorta*). Elevation ranges from 2500-3300 meters above sea level. The climate is continental. Mean annual temperature is 3.8° Celsius, and mean precipitation (mostly from monsoon rains in the summer and snow in the winter) is 94 cm (Colorado Climate Center 2003). The USDA Forest Service (1999) classifies the soil as typic Cryochrepts and Dystrocryepts. Colorado has been hard-hit by the last decade's insect outbreaks in North America. Particularly, bark beetle infestations have been widespread throughout Northern Colorado (Fig. 1,2). Hazardous tree

removal, salvage operations, and active management to potentially alter future forest stand composition have taken place.

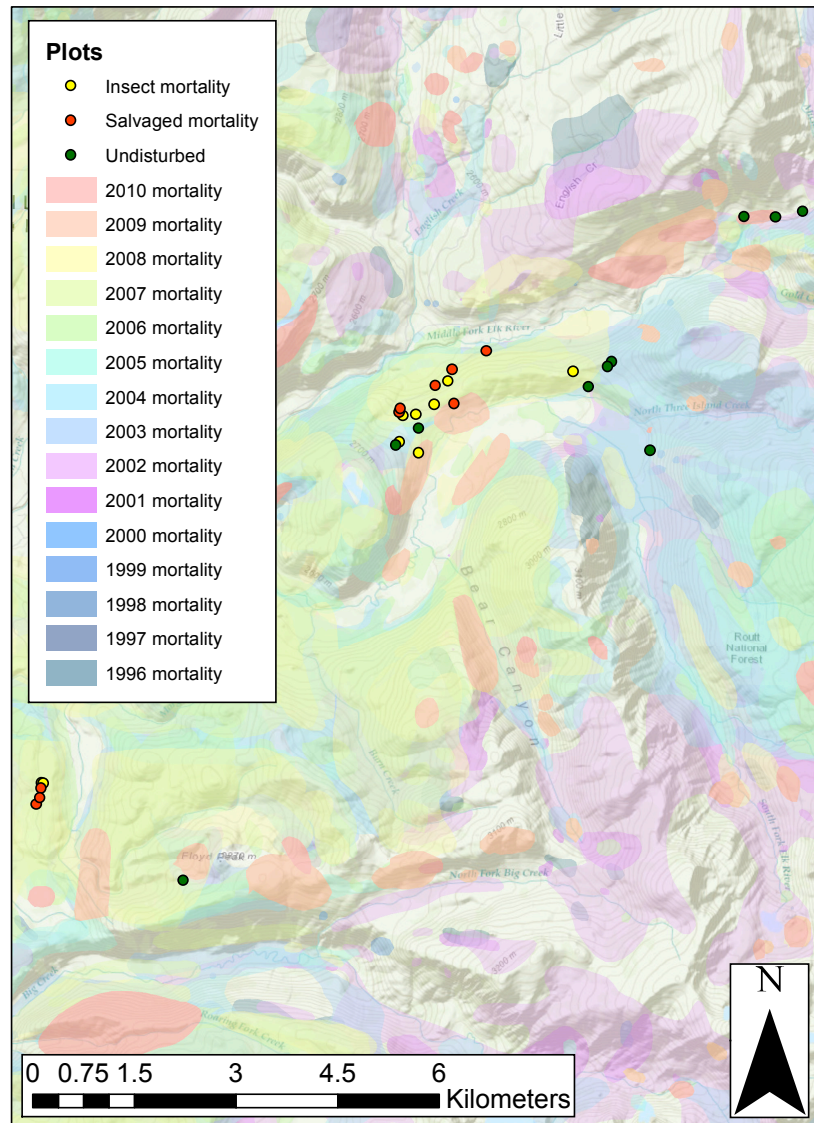


Figure 2: Map displaying study sites on the Routt National Forest (map created by Brian Buma, University of Colorado). Colors indicate year that forest areas were infested by bark beetles. Most of the sites for this study were infested in 2007. Yellow circles indicate plots in the beetle kill treatment; red circles are plots in the logged beetle kill treatment; and green circles are plots in the control group.

Experimental design

Fieldwork took place in the summer of 2012. Ten 15x15 m plots were located in each of the disturbance scenarios (control, beetle kill, and beetle kill/harvested) for a total of 30 plots. All plots were placed in relatively flat areas (less than 5 degree slope) to minimize the effects of slope and aspect. Control plots were those with minimal or no beetle kill, and no salvage logging. Beetle kill plots were selected for grey-stage, close to 100% mortality, and included forests disturbed by both the mountain pine beetle and the spruce beetle. Logged plots were situated at least 100 m from forest edges and away from slash piles associated with logging operations, due to the potential impacts of slash piles on soil properties (Moroni et al. 2009).

Attempts were also made to minimize the effects of pre-disturbance vegetation differences. An ANCOVA of total basal area (including dead trees in the beetle kill treatment) shows that there was not a significant difference in total basal area between the infested treatment and control group. While fir basal area was significantly higher in the beetle kill treatment than control stands ($p < 0.001$), this difference is explained by forest history. Some plots in the beetle kill treatment were infested by bark beetles as early as 2006, resulting in a large amount of well developed advanced regeneration in the beetle kill treatment, which can explain the difference in fir basal area versus the control forests (Fig. 3). There was no significant difference in spruce basal area between the treatment subject to beetle kill and the control. While there was a significantly higher lodgepole basal area in the beetle kill treatment versus the control group ($p < 0.001$), the present study deals

with a subalpine continuum where there is likely to be a gradient of lodgepole presence while Engelmann spruce and subalpine fir remain the dominant canopy species.



Figure 3: Advanced regeneration in beetle kill stands of study area (upper left), intact/green control stands (upper right), and logged beetle kill stands (lower left) (photos by Brooke Regan and Carol Wessman).

Field measurements

Diagonal transects were established to divide each plot into 4 quadrants of equal size for tree and seedling counts. Soil cores at 10 cm depth and fractional cover of understory vegetation (within a 1m² quadrat) were collected at ten randomly located points. The quadrat was gridded in 10x10cm sections to estimate cover for graminoids (grasses), forbs (herbaceous flowering plants), shrubs, bare soil, litter,

moss, roots, rock, and coarse woody debris (Rumbaitis-del Rio, 2006). Soil samples were analyzed for bulk density, organic matter depth, soil moisture, total soil carbon and nitrogen concentration, and soil C:N ratios.

The depth of the duff layer was measured and brushed away before taking the core. The depth of the organic soil layer was measured, and the organic and mineral horizons were separated (labeled “horizon” core). Next to this core, the organic soil was scraped away in order to reach the start of the mineral soil layer and an additional 10 cm core taken (labeled “mineral” core). Soil cores were stored in coolers on ice until transported to the lab, and remained refrigerated until further processing could occur.

Seedlings were counted, identified (by species) and measured for height in each quadrant of the 15x15m plot. Seedlings were characterized as any regeneration less than 150 cm, although it should be noted that this distinction may have included some advanced regeneration. However, this break was made in order to quantify differences in forest understory without having aged forest understory growth. Additionally, it was noted if seedlings were dead or dying.

Larger trees (taller than 150 cm) were measured, counted, and identified by species systematically throughout the plot. Height of trees was measured using a clinometer (in meters), and diameter at breast height was measured using a dbh

tape (in centimeters). Additionally, it was noted if trees were dead or dying, and if so species was still identified based on characteristics of the growth form and bark.

Laboratory Processing

Field moist weights were obtained for the first 5 of the 10 horizon cores from each plot for later bulk density and soil moisture measurements. All samples (1-10 horizon cores from each plot, and 1-10 mineral cores from each plot) were dried at 60°C for 24 hours. After drying, all samples were placed in clean Ziploc bags. The first 5 of the 10 horizon cores were separated from the rest in order to continue processing for bulk density and soil moisture. These horizon cores were sieved through a 2 mm mesh to separate soil into coarse and fine fractions. The coarse and fine fractions for each horizon core were then dried at 105°C for 24 hours.

Following drying, all coarse and fine fractions were removed from the oven, allowed to cool to room temperature, immediately weighed, and stored.

Following drying at 60°C, mineral cores (1-10 from each plot) and remaining horizon cores (6-10 from each plot) were weighed, sieved through a 2-mm mesh, and weighed again (coarse and fine fractions). The coarse fraction was bagged and stored, and the fine fraction ground until no roots or other debris remained.

After grinding, all soil samples were prepared and analyzed in an Edger 1108 CHN elemental analyzer (Carlo-Erba, Milan, Italy) to determine total carbon and total nitrogen concentrations.

Calculations

Bulk density (a measure of soil compaction) was calculated for each sample as the weight of the fine fraction of soil divided by the difference between the volume of the soil horizon of interest and the volume of the coarse fraction of the soil (Culley, 1993). The volume of the soil horizon of interest was assessed via a modified version of the equation for the volume of a cone (the volume of a frustum), $\frac{1}{3}\pi(R^2 + Rr + r^2)$, where R and r were modified based on changing radii associated with the height of the soil horizon, then multiplied by the height of the soil horizon. The volume of the coarse fractions were found using a similar concept to that of water displacement. Coarse fractions were layered in appropriately sized graduated cylinders with salt. Volume was recorded, and then the coarse fraction and salt mixture was sieved through a 1mm mesh. The salt was placed back into the graduated cylinder and volume was recorded. The difference in volumes was recorded as the volume of the coarse fraction. Values for bulk density were reported in grams per cubic centimeter. It should be noted that when calculating average organic and mineral soil bulk densities among plots, those samples within a plot where one of the horizons did not exist were not treated as zeros, because no sample is not equivalent to a value of zero for the bulk density, as this would falsely

lower the average value. The non-existence of organic soil samples was taken into account in calculations of organic horizon mass (see below).

Organic soil moisture was calculated as the difference between the field moist weight and dry weight (dried at 105°C), then weighted by its fraction in the top 10 cm, added to the mineral soil moisture (calculated in the same way), and reported as grams of soil moisture (H₂O) in the top 10 centimeters of soil.

Organic horizon mass was calculated as the product of the bulk density for each organic soil sample and the corresponding depth of that organic soil sample (calculated as g/cm²).

All seedling densities were converted to number of seedlings per hectare (overall and by species). Basal area for trees taller than breast height was calculated as $\pi(\text{dbh}^2)/4$, and reported in total m² for each plot.

Carbon and nitrogen concentration (percentages) were multiplied by a modified calculation of bulk density (that does not correct for the coarse fraction of soil) in order to obtain grams of carbon or nitrogen per cubic centimeter. These values were multiplied by the depth of each organic and mineral horizon (10 cm for all mineral samples), in order to obtain values of carbon and nitrogen for the entire top 10 cm of mineral soil. This value was converted to Mg/Ha (Sollins et al. 1999).

Data Analysis

The primary objective of the analyses was to determine if there were treatment differences (beetle kill, logged beetle kill, and control) in soil physical and chemical variables, as well as seedling densities and percent cover of forest understory. The R program (R Core Team, 2012) was used for statistical analyses. Analysis of covariance (ANCOVA) models tested for interactions among topographic variables (slope, aspect, and elevation) and interactions among topographic variables and treatment. Tukey's HSD post-hoc tests were used to determine where differences in adjusted means of each treatment occurred. For analysis of all bulk density calculations, soil moisture, soil horizon depths, and organic horizon mass, the data for two highly anomalous logged plots were removed, as they were extreme outliers with respect to the values for these soil physical variables.

RESULTS

Soil physical properties

The calculated values for bulk density in the top 10 cm (g/cm^3) showed significant differences in the ANCOVA, with strong differences among treatments ($F_2=7.163$, $p<0.01$). Specifically, there was a strong significant difference between the logged treatment and the other two treatments ($p<0.01$), with the logged treatment displaying higher bulk density (mean= $0.58 \text{ g}/\text{cm}^3$) (Fig. 4). In the ANCOVA for organic and mineral soil bulk density, there was no statistically significant difference between treatments (Fig. 5).

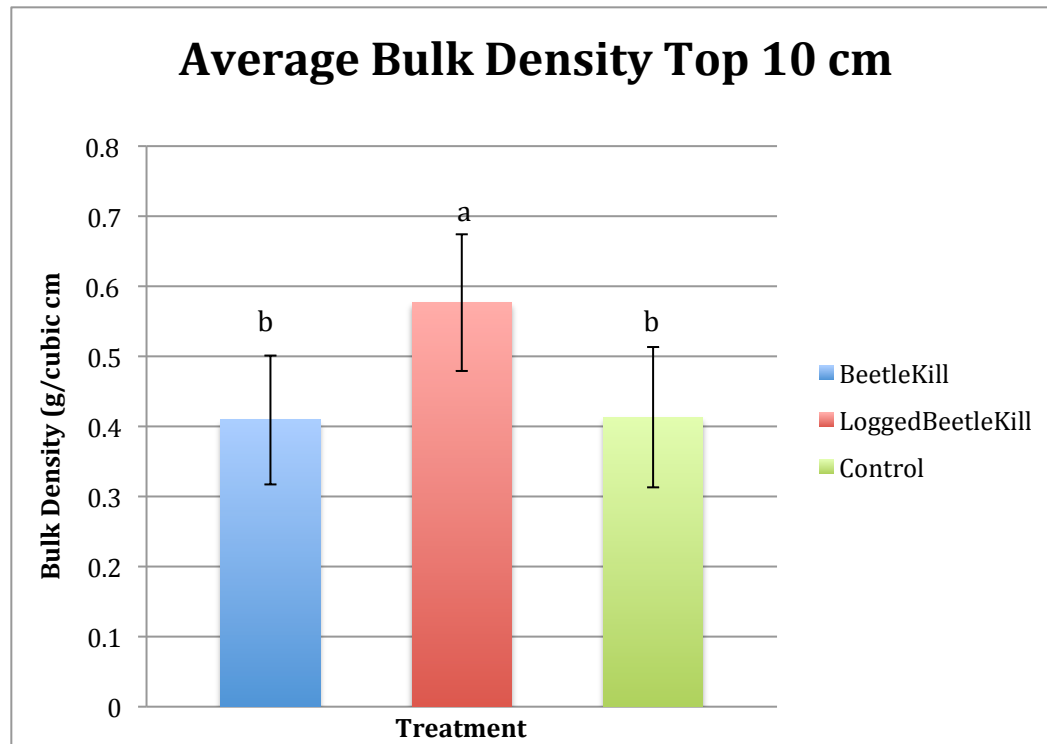


Figure 4: Average bulk density for the top 10 cm of soil in each treatment (± 1 s.d.), reported in g/cm³. The ANCOVA showed a significant difference among treatments ($F_2=7.163$, $p<.01$). Small letters denote differences among treatments.

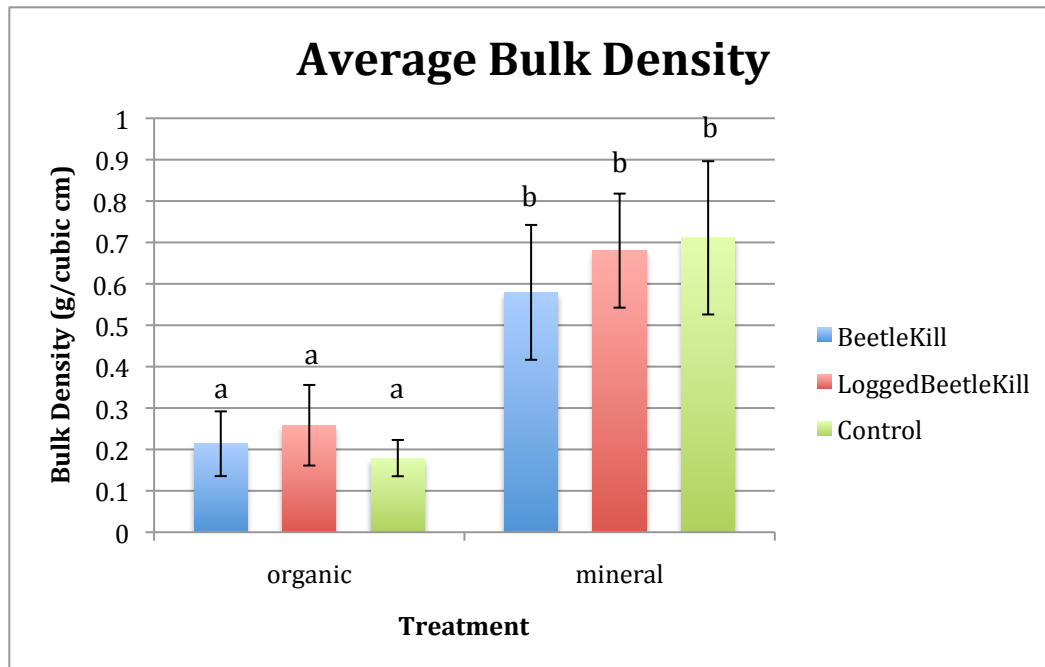


Figure 5: Average mineral and organic soil bulk density in each treatment (+/- 1 s.d.), reported in g/cm³. There were no significant differences among treatments.

Soil moisture was influenced by aspect in the logged plots to some degree $F_{11,18} = 2.036$, $p < 0.05$, however, there was still a significant treatment effect ($F_{(2)} = 4.774$, $p < 0.05$). The logged treatment (mean = 34.25 gH₂O/total gDry soil) showed significantly higher soil moisture than the beetle kill treatment ($p < 0.05$), while in the comparison of logged and control treatments ($p = 0.09$). The beetle kill treatment and control treatment were similar ($p = 0.748$) in values of soil moisture (Fig. 6).

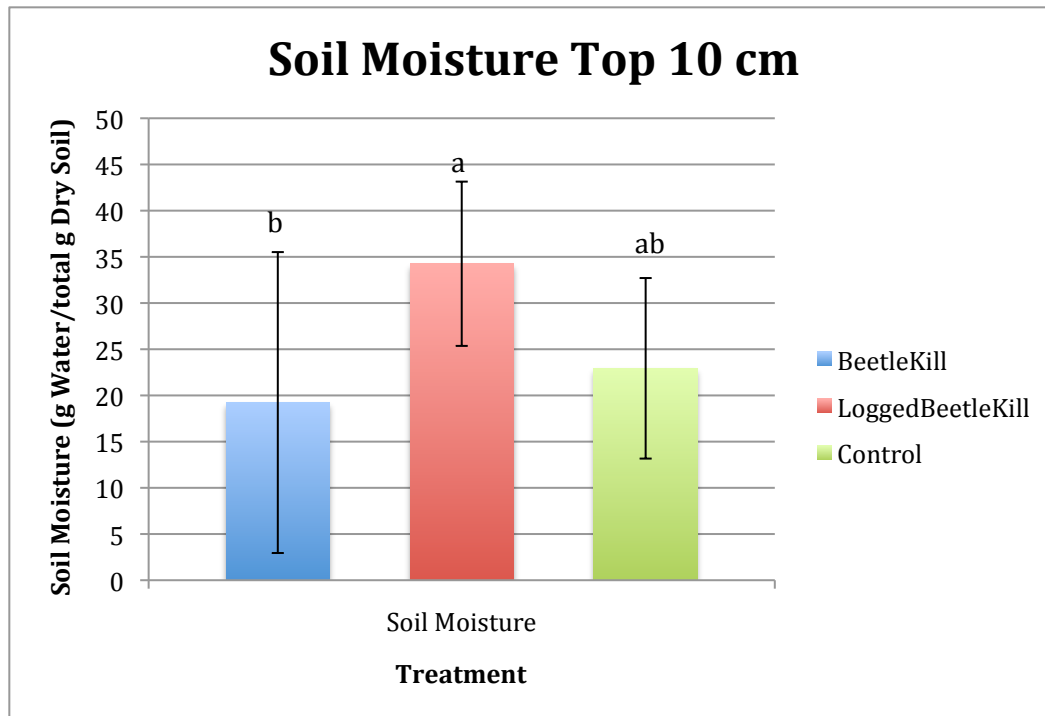


Figure 6: Average soil moisture for the top 10 cm of soil in each treatment (± 1 s.d.), reported in grams of water per total grams of dry soil. The ANCOVA showed significant differences among treatments ($F_2=4.774$, $p<0.05$). Small letters denote differences among treatments.

The ANCOVA for organic horizon mass showed a significant treatment effect ($F_2=4.25$, $p<0.05$). Specifically, the logged treatment had a significantly lower organic horizon mass (mean=41.71 Mg/Ha) than the control treatment ($p<0.05$) and slightly lower than the beetle kill treatment ($p=0.087$), while the control and beetle kill treatments were similar ($p=0.89$) (Fig. 7).

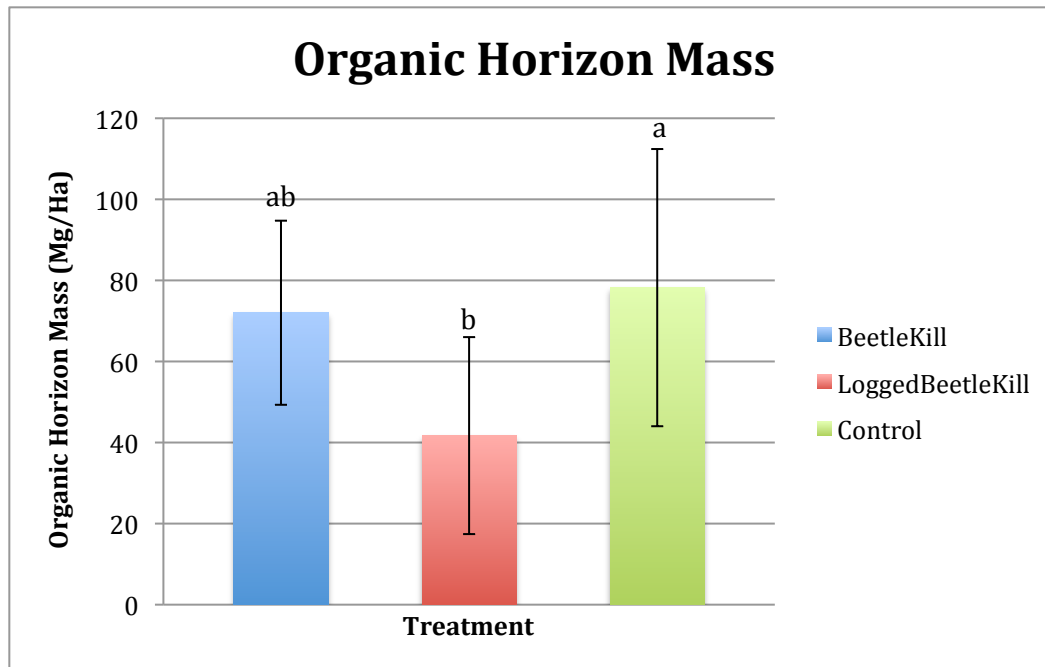


Figure 7: Average organic horizon mass (Mg/Ha) in each treatment (\pm 1 s.d.). The ANCOVA showed a significant difference among treatments ($F_2=4.25$, $p<0.05$). Small letters denote differences among treatments.

When looking at soil horizon depths, there was a slight significant difference among treatments in the depth of the duff layer ($F_2=4.080$, $p<0.05$); specifically, logged and control treatments ($p=0.055$, logged duff was slightly lower, mean=1.63 cm); logged and beetle kill treatments ($p=0.061$). There was no significant difference between the beetle kill and control treatments. There was a treatment effect for organic soil ($F_2=10.092$, $p<0.01$). Specifically, logged organic soil was, on average, significantly shallower (mean=1.96 cm) than beetle kill or control treatments (respectively $p<0.05$, $p<0.01$). Additionally, there was a strong treatment effect of the depth of mineral soil ($F_2=17.146$, $p<0.001$). Specifically, the mineral soil in the logged treatment composed significantly more of the top 10 cm (mean= 8.13 cm) than the beetle kill mineral soil ($p<0.01$), and the control mineral soil ($p<0.001$) (Fig. 8).

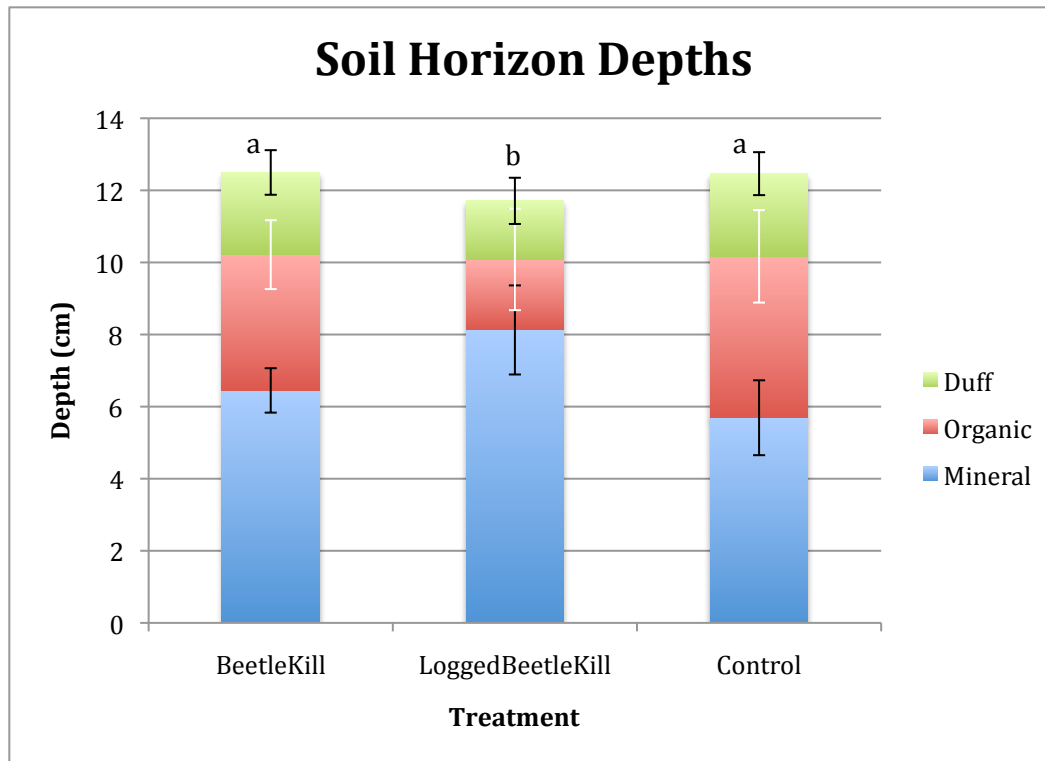


Figure 8: Average soil horizon depths (in cm) for each treatment (+/- 1 s.d). The ANCOVA showed significant differences in soil depths among treatments for duff ($F_2=4.080$, $p<0.05$), organic ($F_2=10.092$, $p<0.01$), and mineral ($F_2=17.146$, $p<0.001$). Small letters denote differences among treatments for all three horizons.

Soil chemical properties

Aspect had an influence on carbon in the top 10 cm of mineral soil in the control treatment ($F_{11,18}= 3.413$, $p<0.05$). When aspect was controlled for in the ANCOVA, there were significant differences in carbon (Mg/Ha) among treatments ($F_2=10.6270$, $p<0.001$). Specifically, the control group had significantly higher mineral soil carbon (mean= 31.91 Mg/Ha) than the beetle kill ($p<0.001$) and logged treatments ($p<0.01$) (Fig. 9). Nitrogen was influenced by aspect in the control treatment as well ($F_{11,18}=3.892$, $p<0.05$), however, the same trend for carbon existed for differences among treatments in nitrogen (Mg/Ha) in the top 10 cm ($F_2= 13.427$,

$p < 0.001$). Specifically, the control treatment had significantly higher mineral soil nitrogen (mean = 1.334 Mg/Ha) than the beetle kill ($p < 0.001$) or logged ($p < 0.01$) treatments (Fig. 10). Analyses of carbon and nitrogen in organic soil, as well as C:N ratios in organic and mineral soil, showed no statistically significant differences among treatments and figures are not shown.

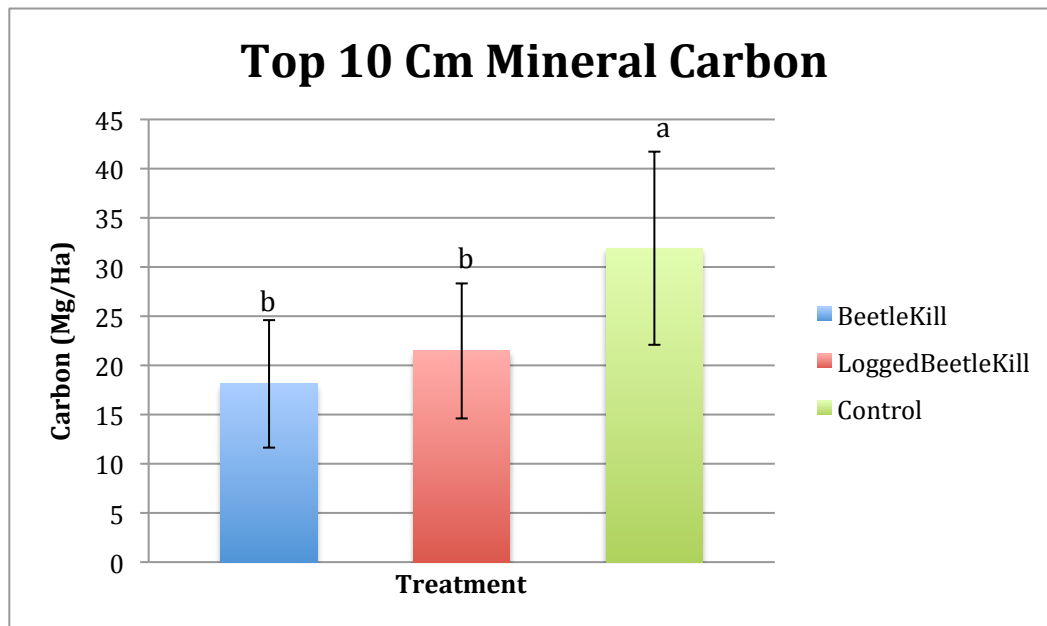


Figure 9: Average carbon (Mg/Ha) of the top 10 cm of mineral soil in each treatment (+/- 1 s.d.). The ANCOVA showed a significant difference in treatments ($F_2 = 10.627$, $p < 0.001$). Small letters denote differences among treatments.

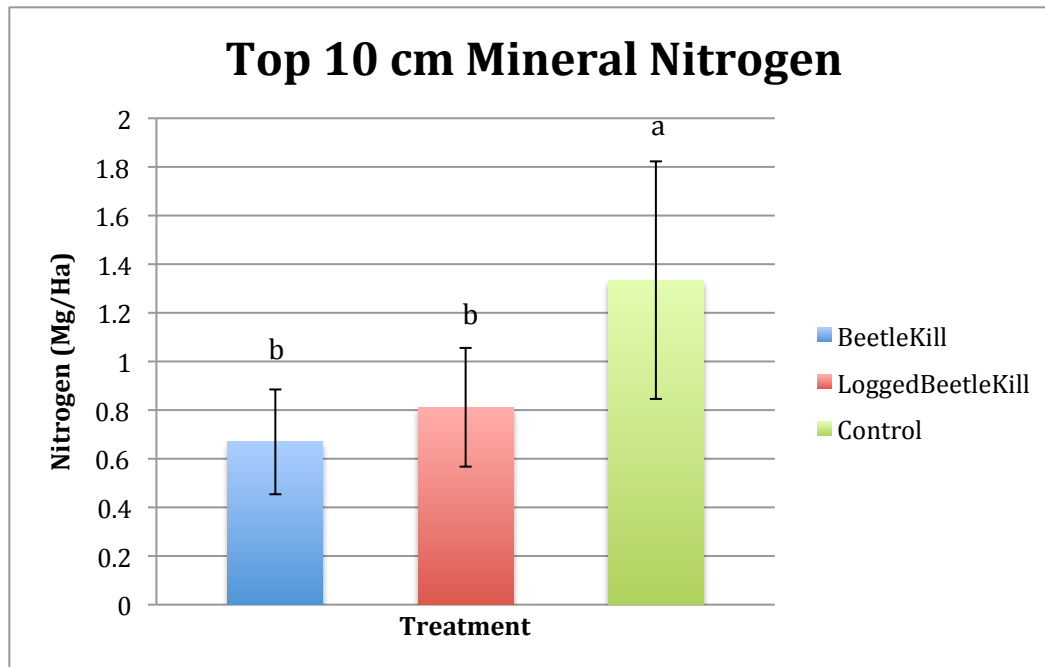


Figure 10: Average nitrogen (Mg/Ha) of the top 10 cm of mineral soil in each treatment (+/- 1 s.d.). The ANCOVA showed a significant difference in treatments ($F_2 = 13.427$, $p < .001$). Small letters denote differences among treatments.

Forest regeneration/Forest understory

ANCOVA showed a significant treatment effect ($F_2 = 4.917$, $p < 0.05$) for total seedling density (Fig. 11). Specifically, the beetle kill treatment had a significantly higher seedling density (mean = 7946.7 seedlings/Ha) than the control treatment ($p < 0.05$); logged and beetle kill treatments ($p = .090$) and logged and control treatments ($p = 0.723$) were not significantly different. When differentiating seedling densities among species, the only species in which there were statistically significant differences among treatments was subalpine fir ($F_2 = 5.287$, $p < 0.05$). The beetle kill treatment had a significantly higher fir seedling density than the control or logged treatments (mean (beetle kill) = 6893.3 seedlings/Ha, $p < 0.05$ and $p = 0.058$, respectively) (Fig. 12). In the logged treatment, an average of 10% of total fir

seedlings were dead (compared to 0% in the beetle kill treatment and 0.4% in the control treatment).

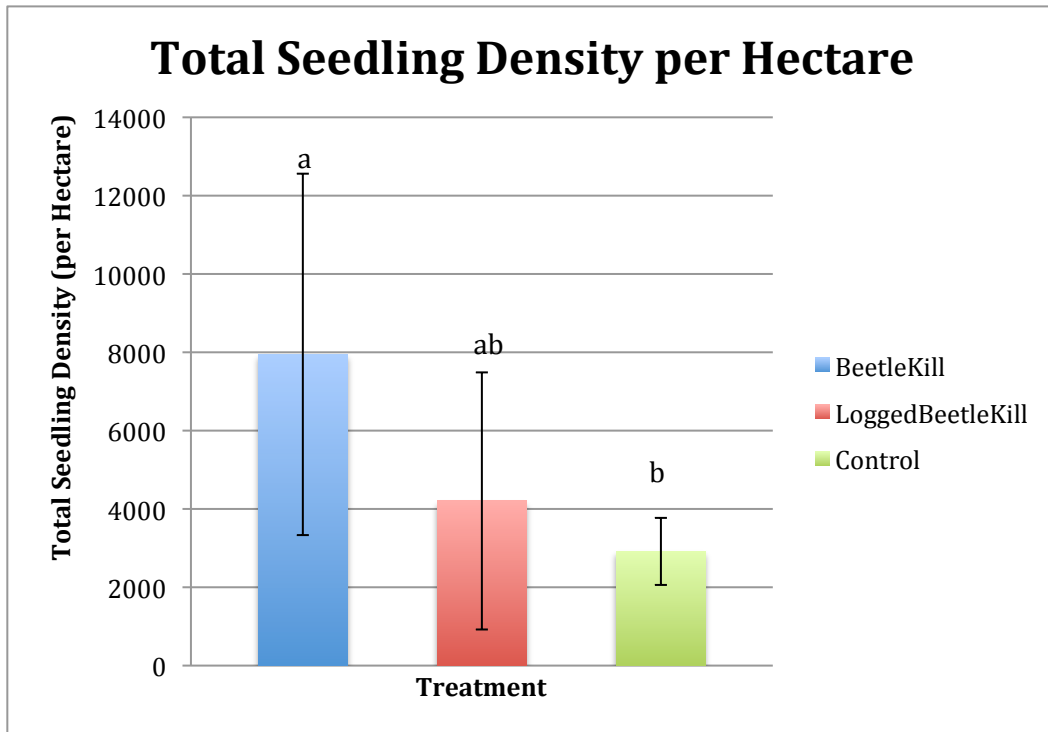


Figure 11: Total seedling density (of all species) per hectare in each treatment. The ANCOVA showed a significant difference among treatments ($F_2=4.917$, $p<0.05$). Small letters denote differences among treatments.

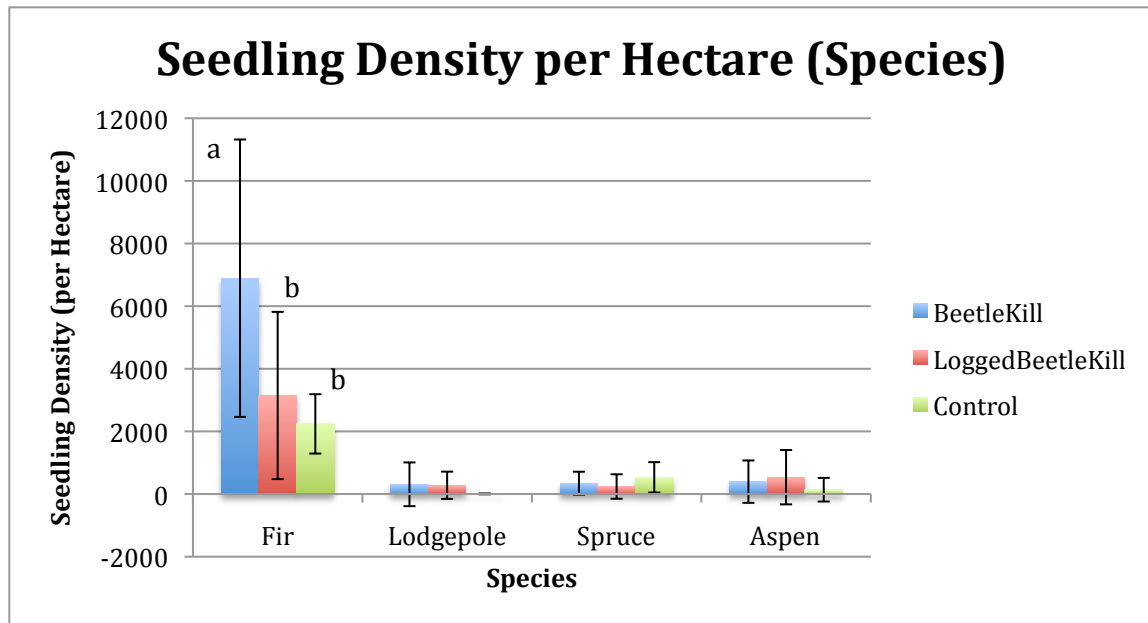


Figure 12: Seedling density per hectare for each treatment, by species. The ANCOVA showed no differences among treatments in lodgepole, spruce, or aspen, but a significant difference among treatments in fir ($F_2=5.287$, $p<0.05$). Small letters denote differences among treatments.

Percent of forbs in the forest understory were influenced by slope ($F_{(11,18)}=2.27$, $p<0.05$), particularly slope in the control group ($F_{(11,18)}=2.27$, $p<0.05$). However, when controlling for these effects in the ANCOVA, there was still a strong difference among treatments ($F_2=7.780$, $p<0.01$) (Fig. 13). Particularly, forbs composed a significantly lower percentage in the logged treatment (mean=12.6%) than the beetle kill or control treatments ($p<0.05$, $p<0.01$ respectively; Fig. 13). Fractional cover of shrubs was influenced by slope in the logged treatment $F_{11,18}= 2.105$, $p<0.05$. After controlling for this in the ANCOVA, there was still a treatment effect ($F_2= 3.918$, $p<0.05$). However, Tukey's HSD (a conservative post-hoc test) showed only slightly significant differences, with the logged treatment being slightly higher (mean=0.4%, $p=0.06$) than the beetle kill or control treatments. There was a strong

treatment effect for the fraction of coarse woody debris in the forest understory ($F_2 = 23.482$, $p < 0.001$). Specifically, the logged treatment had much higher percentage of coarse woody debris in the understory (mean=38.9%) than the beetle kill or control treatments ($p < 0.001$) (Fig. 13). All other components of the forest understory were not significantly different among treatments.

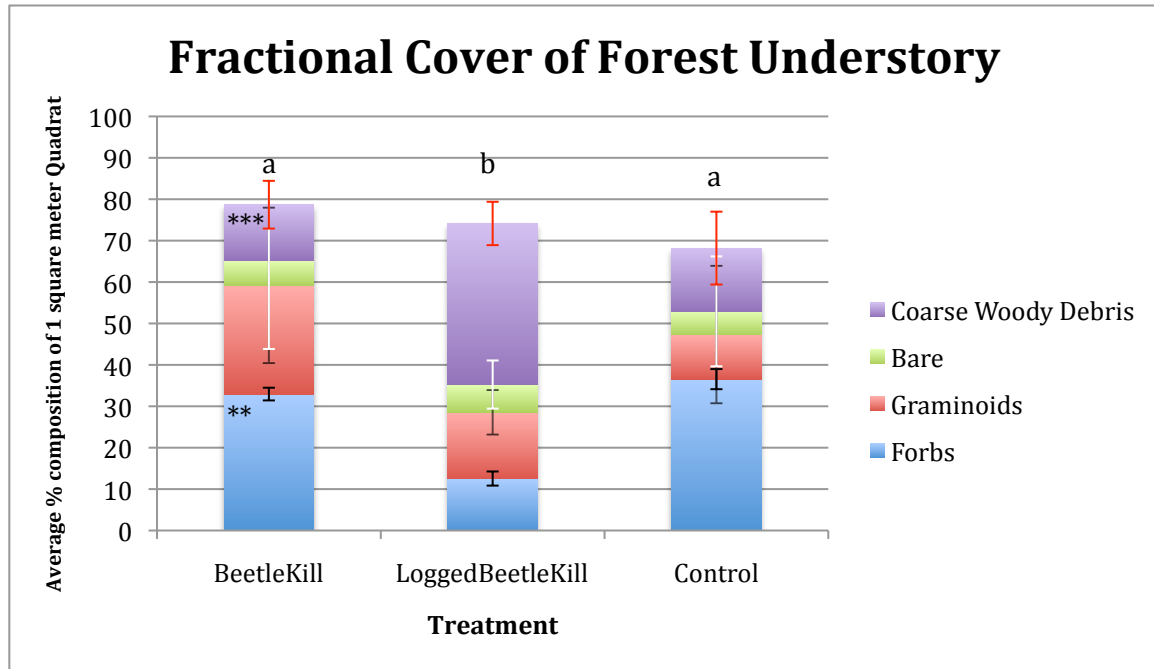


Figure 13: Average percent cover of forbs, shrubs, and coarse woody debris in a 1 m² quadrat. Values do not equal 100 % because this figure does not include percent cover of seedling species, litter, rock, shrubs (due to percentages being too small at this scale), moss, or roots. Small letters denote differences among treatments and stars denote those specific items where significant differences were found.

Table 1. Results of the ANCOVAs for each variable of interest where significant treatment effects were found. Appendix 1 summarizes all results.

Treatment Relationships of Each Variable of Interest

Variable	Beetle Kill	Logged BK	Control	ANCOVA result (Treatment significance level)
Bulk Density (g/cm ³) (Top 10 cm)	b	a	b	**
Soil moisture (gH ₂ O/total gDry) (Top 10 cm)	b	a	ab	*
Organic Horizon Mass (g/cm ²)	ab	b	a	*
Duff (cm)	a	b	a	*
Organic (cm)	a	b	a	**
Mineral (cm)	a	b	a	***
Total Seedling Density (per hectare)	a	ab	b	*
Fir Seedling Density (per hectare)	a	b	b	*
Forbs (% per m ²)	a	b	a	**
Shrubs (% per m ²)	a	b	a	*
Coarse Woody Debris (% per m ²)	a	b	a	***
Mineral Soil Carbon (Mg/Ha)	b	b	a	***
Mineral Soil Nitrogen (Mg/Ha)	b	b	a	***

DISCUSSION/CONCLUSIONS

General Findings

The present findings indicate that harvesting of beetle kill forests in the subalpine ecosystem studied impacts certain soil properties, as well as forest regeneration, beyond the properties associated with the beetle kill disturbance alone. A mixed forest type, such as in the present study, shows the highest post-disturbance basal area and seedling density (of all overstory types impacted by bark beetles) (Diskin et al. 2011). Additionally, previous findings have found that alteration of soil properties associated with beetle kill are relatively minor considering the broad extent of the outbreaks (Griffin et al. 2011). However, as I have found here, 6 years after initial beetle infestation, soil physical properties do not differ between beetle kill and control stands, while stocks of carbon and nitrogen differ dramatically. More importantly, logging appears to alter soil physical properties, but not carbon or nitrogen stocks.

Soil Physical Properties

Overall, soil physical characteristics of beetle kill stands are not significantly different from what they would be in an intact, green forest (i.e. the control group). This lack of effect may be attributable to a minimum of 6 years having passed since these forest stands were first infested by beetles, allowing time for the large amount of dead needles added to the forest understory to decompose under the typically moist conditions of this region (Fogel and Cromack 1977). With regard to soil moisture, while Clow et al. (2011) attributed higher soil moisture under beetle kill

trees to reduced evapotranspiration when compared to healthy trees, that study was conducted in a montane forest dominated by lodgepole pine. In contrast, we see that in the present study, in a true subalpine ecosystem, where intact green forests are moister than they would be in a montane system, the beetle kill disturbance is not changing this soil physical property.

However, it appears as though harvesting may disrupt the state of soil physical properties. Soil is more compacted, and surprisingly moister in the logged beetle kill treatment than the treatment subject only to beetle kill. The compaction of the top 10 cm of soil in the logged treatment can perhaps be explained by logging equipment and practices, as the disruption of the forest floor surface layer associated with harvesting systems is relatively well known. The higher values for soil moisture in the logged beetle kill treatment versus the beetle kill treatment alone are harder to explain. The northern Routt National Forest is an area that receives a high amount of moisture (in the form of snow) relative to other portions of the state of Colorado. Moister plots in the logged treatment could perhaps be related to stronger capture of snow moisture, due to total loss of forest canopy, especially in low to average snow years where snow might not fully penetrate the canopy structure associated with beetle kill forests (Boon, 2012). Another possibility for moister soils in the logged beetle kill treatment could be the total reduction in evapotranspiration resulting from a total loss of the forest canopy.

The slightly lower organic horizon mass in the logged treatment, coupled with the shallower organic horizon, can perhaps be explained by the disruption of forest understory associated with logging equipment. Harvesting practices often result in the removal/loss of forest floor biomass (Binkley and Fisher 2013), and Nave et al. (2010) summarizes over hundreds of studies, indicating that forest harvesting leads to a decline in organic horizon mass of approximately 30%.

While the impacts of organic soil removal and soil compaction on a forest have been found to be highly variable (Binkley and Fisher 2013), it is important to consider whether the alteration of these soil properties will have long term decreases in forest productivity. It may be the case that these soil properties are altered only temporarily, with no resulting decrease in site productivity (Powers et al. 2005). This could be attributed to no actual loss in soil organic matter (Binkley and Fisher 2013). However, answering this question is beyond the scope of the present study, and yet is important to consider.

Soil Chemical Properties

No differences were found in carbon and nitrogen pools of the organic soil layer, or C:N ratios in the organic soil or mineral soil layers among the treatments subject to beetle kill, the logged beetle kill treatment, or the control group. C:N ratios are an important measure of nitrogen mineralization rate, as the amount of nitrogen accumulated in the soil in a given amount of time. This is important for meeting soil microbe requirements for nitrogen, and is the form of nitrogen used by vegetation.

So, normal C:N ratios in the harvested and beetle kill treatments is a positive finding, thus indicating that timber harvest does not further negatively impact beetle kill forests with regard to soil carbon and nitrogen.

However, the control group carbon and nitrogen pools of the top 10 cm of mineral soil far exceeded those of either the beetle kill treatment or the logged beetle kill treatment. The lower than expected values for carbon and nitrogen in the treatment subject to beetle kill may be explained by the increased understory light levels associated with the death of the forest canopy. Such conditions can result in increased microbial respiration, resulting in decomposition of carbon from fallen needles. Harvest practices may result in incorporation of organic soil into mineral soil (Binkley and Fisher 2013), perhaps explaining the lack of carbon and nitrogen loss associated with timber harvest (and thus explaining the higher than expected carbon and nitrogen values in the logged beetle kill treatment). Carbon and nitrogen pools are an important component to the cycling of nutrients in an ecosystem.

Forest Succession/Forest Understory

Present findings suggest that subalpine fir seedlings are dominating these subalpine forests disturbed by bark beetles (characterized by a lodgepole- spruce –fir overstory, infested by both mountain pine beetle and spruce beetle), compared to logged beetle kill forests and intact/green forests, with results indicating that logging may inhibit or damage this subalpine fir growth. This finding is consistent

with subalpine fir dominance associated with spruce beetle infestation (Veblen et al. 1991) and mountain pine beetle infestation (Diskin et al. 2011). Diskin et al. (2011) point out that there is a lack of uniformity in how various lodgepole forest types are responding to mountain pine beetle disturbance. Here, we see that in a truly subalpine mixed forest (also impacted by spruce beetle), with a forest canopy containing lodgepole, spruce, and fir, there is major regrowth and accelerated growth of subalpine fir, while this growth is altered and disrupted when beetle kill stands are logged. Additionally, the large amount of advanced regeneration associated with beetle kill forests no longer exists in the harvested stands and there may be death of up to 10% of previously existing subalpine fir seedlings. It also appears to be the case that, at least in the early stages of regrowth, logging of these forests does not favor any sort of alternative successional trajectory.

Specifically, while Collins et al. (2011) found that lodgepole pine is the dominant species regenerating in logged beetle kill stands, perhaps this is not the case here due to the difference in forest canopy structure prior to disturbance. The study by Collins et al. (2011) was conducted in a subalpine ecosystem where the forest canopy is co-dominated by lodgepole pine. Here, we see that in a forest canopy of predominately subalpine fir and Engelmann spruce, (with a minor component of lodgepole pine), lodgepole pine seed sources may be relatively limited and conditions may not be favorable to lodgepole pine seedling establishment. For example, unexpectedly moist conditions in the logged beetle kill treatment found

here may not be suitable for lodgepole pine that are adapted to drier, more exposed conditions (Lotan, 1964; Lotan 1975; Lotan and Perry 1983).

Another important consideration is the serotinous property of many lodgepole pine cones. Aoki et al. (2011) found that time since disturbance likely does not impair seed longevity in serotinous lodgepole pine cones, which can release their seeds through contact with soil surface heat (Tower 1909; Lotan 1964). The lodgepole cones in the present study area may, however, be non-serotinous, releasing their seeds as cones mature (which does not leave much in terms of seed availability for forest regeneration).

These three possibilities (soil moisture, pre-disturbance canopy differences, and non-serotinous cones) for lack of lodgepole establishment post harvest suggest that the ecosystem studied here will not favor regrowth of lodgepole pine after infestation by mountain pine beetle, even if stands are harvested.

On the other hand, there may be additional factors explaining why lodgepole pine seedlings are not proliferating in the logged beetle kill treatment. It has been personally observed in the present study area that following logging of blowdown areas lodgepole pine does not establish until 3-4 years after the logging has occurred (C. Wessman et al.). So, it would be important to follow up the present study in several years to determine whether there is a similar lag in lodgepole pine establishment following harvest of beetle kill stands. The implication of finding

such a lag would be that an alternative trajectory of lodgepole pine establishment is likely being favored in harvested subalpine fir stands of high beetle induced mortality.

The high prevalence of coarse woody debris in the logged treatment compared to the other two groups is likely indicative of logging practices, and could have implications for forest fuel loads (Collins et al. 2012). The significantly higher percentage of forest understory composed of forbs in the treatment subject to beetle kill and the control group indicate that there is not a barrier to forb regrowth associated with beetle kill disturbance. However, logging beetle kill forests potentially disrupts soil and creates light conditions that alter this regrowth. This change in conditions may explain the slightly higher percentage of shrub growth in the logged treatment than the beetle kill or control treatments. Again, we see that harvesting of these beetle kill forests potentially alters conditions such that these changes occur.

Limitations of Study/Future Directions

It may be hard to fully understand widespread stand responses to beetle kill and logging at such a relatively small scale (30 plots). In order to understand what land management strategies will be most fitting for these forests, it will be important to develop future understanding of the epidemic impacts at landscape scales.

Additionally, there may have been confounding effects of pre-disturbance vegetation differences, as this is a challenging variable to control for in a mixed subalpine ecosystem. Future studies should effectively minimize these pre-disturbance differences among treatments.

Study Importance

The impacts of harvesting forests of high beetle induced mortality have implications for resource management as agencies utilize different portions of forest for different purposes. This leaves managers with decisions about which areas should be salvaged after a disturbance, and which portions should be left to natural responses. To make these decisions, forest managers must understand how components of the ecosystem are affected by logging. Understanding how the forest is likely to respond to multiple disturbances is crucial to enhancing the future resilience of this forest. Similar to Diskin et al. 2011, I conclude that proactive management efforts in beetle kill forests are unnecessary and may, in fact, change important soil properties vital to the ability of seedlings to grow in the forest ecosystem. Not only this, but as of now, there does not appear to be an alternative successional trajectory favored by harvesting efforts, which in some instances may be counter to management objectives. While hazard tree removal may clearly be necessary, perhaps salvage logging efforts can be conducted with these impacts in mind.

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APPENDIX 1: Summary of means, standard deviations, and ANCOVA significance levels for all soil physical and chemical variables, as well as forest regeneration and forest understory composition.

Variable	Beetle Kill (mean, +/- 1 s.d)	Logged BK (mean, +/- 1 s.d)	Control (mean, +/- 1 s.d)	ANCOVA result
Organic Bulk Density (g/cm ³)	0.214, 0.078	0.258, 0.097	0.179, 0.044	n.s.
Mineral Bulk Density (g/cm ³)	0.579, 0.163	0.680, 0.138	0.711, 0.185	n.s.
Bulk Density Top 10 cm (g/cm ³)	0.409, 0.092	0.577, 0.097	0.413, 0.100	**
Soil Moisture Top 10 cm (gWater/totalgDry)	19.231, 16.285	34.252, 8.891	22.936, 9.771	*
Organic Horizon Mass (g/cm ²)	72.070, 22.710	41.712, 24.298	78.217, 34.194	*
Duff depth (cm)	2.28, 0.619	1.625, 0.641	2.299, 0.596	*
Organic depth (cm)	3.767, 0.955	1.956, 1.407	4.478, 1.283	**
Mineral depth (cm)	6.449, 0.616	8.127, 1.236	5.691, 1.039	***
Total Seedling density (per Ha)	7946.667, 4614.184	4204.444, 3282.423	2915.556, 855.984	*
Fir Seedling density (per Ha)	6893.333, 4428.785	3146.667, 2670.351	2240, 947.963	*
Spruce seedling density (per Ha)	346.667, 365.779	240, 390.954	533.333, 485.058	n.s.
Lodgepole seedling density (per Ha)	311.111, 698.656	280, 435.490	4.444, 14.055	n.s.
Aspen seedling density (per Ha)	395.556, 676.779	537.778, 867.508	137.778, 377.385	n.s.

Rock % Cover (1 m ²)	1.21, 1.533	1.45, 1.707	2.444, 2.428	n.s.
Forb % Cover (1 m ²)	32.95, 18.754	12.55, 5.382	36.556, 16.582	**
Gramminoid % Cover (1 m ²)	26.25, 21.352	16, 5.817	10.767, 13.277	n.s.
Bare % Cover (1 m ²)	6, 5.761	6.7, 5.234	5.6, 8.799	n.s.
Coarse Woody Debris % Cover (1 m ²)	13.48, 10.746	38.9, 6.822	15.278, 7.540	***
Litter % Cover (1 m ²)	14.61, 11.892	18.85, 11.664	20.689, 17.374	n.s.
Shrubs % Cover (1 m ²)	0, 0	0.4, 0.699	0,0	*
Moss % Cover (1 m ²)	0, 0	0, 0	1.589, 3.403	n.s.
Roots % Cover (1 m ²)	0, 0	0, 0	0.056, 0.167	n.s.
Mineral soil carbon (Mg/Ha)	18.119, 6.480	21.468, 6.862	31.909, 9.817	***
Mineral soil nitrogen (Mg/Ha)	0.669, 0.216	0.812, 0.244	1.334, 0.488	***
Organic soil carbon (Mg/Ha)	17.895, 11.149	12.953, 8.262	17.555, 6.271	n.s.
Organic soil nitrogen (Mg/Ha)	0.532, 0.323	0.378, 0.231	0.612, 0.233	n.s.
Mineral soil C:N	26.373, 2.897	25.574, 3.124	24.211, 4.034	n.s.
Organic soil C:N	32.278, 4.914	25.489, 14.409	28.408, 4.823	n.s.